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Variation in *Francolinus adspersus* Waterhouse, 1838, of the South West Arid Zone of Africa

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Abstract. The Red-billed Francolin *Francolinus adspersus* is the most xeric of a group of three ventrally scaled or barred phasianids more or less confined to the Southern African Subregion. Shown as exhibiting a measure of variation by R. Meyer de Schauensee in 1931 on the basis of a small sample from the Lake Ngami region of Botswana, few other authors have recognised *F. adspersus* as being other than a monotypic species. A re-examination of the case shows that the pale phenotypes named as *F. a. kalahari* are not confined to northern Botswana, but extend west to north-western Namibia and the mid- and lower Kunene R. valley of Angola, and effectively split the darker populations, which constitute the nominate race of de Schauensee. The males of the latter are also now found to range larger in size than those of the pallid, more desertic, population named *kalahari*. On the basis of a now enlarged range of characters, including a mensural one, and the determining of acceptable ranges for both pale (and small) and dark (and large) forms, the Red-billed Francolin requires to be seen as a polytypic species.

Key words. Francolins, monotypic, substrate colour response, arid zone, polytypic status.

The Red-billed Francolin *Francolinus adspersus* Waterhouse, 1838, of the northern and north-eastern aspects of the South West Arid Zone is one of a complex of three largely allopatric scaled and barred francolins centred in the south of the African continent. It was initially discovered during General Sir J. E. Alexander's 1830s expedition to what is today Namibia, and is distributed from central and northern Namibia and the drier parts of south-western Angola, east north of the Kalahari desert of Botswana to the mid-Zambesi valley of south-western Zambia and the north-west of Zimbabwe, where it meets and is then replaced by the Natal Francolin *Francolinus natalensis* Smith, 1834, to the east and south-east.

The Red-billed Francolin affects dry acacia and mixed bushveld vegetational types, and examination of the relevant map in Snow (1978) shows that records are largely clustered along the major rivers impinging on the northern districts of the arid zone, such as the Kunene, Okavango and mid-Zambezi. On the basis of Alexander's account of his expedition, Macdonald (1951) restricted the type-locality to the upper Kuiseb River in western Damaraland on the edge of the plateau. The species is generally viewed as monotypic, but as long ago as 1931 Meyer de Schauensee demonstrated that it showed a measure of geographical variation when he described *F. a. kalahari*, based on a small sample of three specimens from Lake Ngami, Botswana, as discrete from the central Namibian population on a whiter throat, more strongly barred upper mantle and hind neck, and greyer pileum and dorsal surface; also on a slightly smaller bill. The name employed is singularly inapposite, as the present francolin does not normally occur in the largely waterless Kalahari region.

Table 1: The size differential (in mm) as demonstrated by wing-length in two population groupings in the Red-billed Francolin.

Population	age class	n	male range	\bar{x}	s. d.	age class	n	female range	\bar{x}	s. d.
1. Gt Namaqualand — Damara-land, Namibia	ad.	11	191—201	195.0	4.26	ad.	9	170—177.5	173.3	1.91
	1st y.	11	178—188	183.8	3.54	1st y.	2	160, 164	—	—
2. N. W. Zimbabwe, adj. Botswana and S. W. Zambia	ad.	7	182—190	186.1	3.02	ad.	4	174—180	175.5	—
	1st y.	2	174, 176	—	—	1st y.	5	160—167	165.4	3.04
3. N. W. Botswana, N. E. Namibia & Caprivi Strip	ad.	3	180—190	183.5	—	ad.	3	170—177	173.3	—
	1st y.	5	170.5—177	173.0	3.04	1st y.	6	160—168	163.3	3.44
4. Kaokoland, N. W. Namibia	ad.	2	179, 180	—	—	ad.	2	173, 174	—	—
	1st y.	2	170, 177.5	—	—	1st y.	7	159—165	163.0	2.23
5. S. Angola (after Rosa Pinto (1983))	ad. &	—	159—191	—	—	ad. &	—	163—170	—	—
	1st y.	—	(in 30 measured)	—	—	1st y.	—	—	—	—

12 ad. σ from populations 2—4, wings 179—190 (184.3), s. d. 4.16, in 9 1st y. 170—177.5 (173.6), s. d. 3.01; wings in 9 σ ads 170—180 (174.3), s. d. 2.82, in 18 1st y. 159—168 (163.7), s. d. 2.92.

C. D. between ad. σ (n = 12) pf Nos 2—4 compared with No. 1 = 1.27 (joint nonoverlap 89/90 %).

C. D. between 1st y. σ of Nos 2—4 (n = 9) and No. 1 (n = 11) 1.42.

Namibian plateau males (*F. a. adspersus*) are statistically larger than in *F. a. kalahari*, particularly when in sub-adult (1st year) dress (population 1). By contrast, females do not range significantly larger, except in respect of variation in tail-length, which in population 1 ranges greater: 90—93.5, versus 83.5—87 mm in *kalahari*. In *F. adspersus* sub-adult males agree closely in their dimensions with their respective adult females, but carry rudimentary spurs, while sub-adult females are shorter winged than either. Note also that population 2 and of the eastern Caprivi Strip of Namibia (population 3) are part of the taxon *F. a. adspersus*.

While *F. a. kalahari* is seldom recognised, it was listed in the Southern African Checklist (Clancey 1980), largely on the basis of greyer upper-parts and rather smaller bill. A recent re-examination of the issue reveals that variation in colour is slight, populations inhabiting desertic country generally paler and rather more greyish buffy brown on the vertex and over the upper-parts and adjacent wing surfaces, the dark grey ventral barring on the whole finer with whiter light interstices than birds of mesic plateau. Such desertic differentiates are not peculiar, however, to the northern parts of Botswana, but extend far to the west to reach Kaokoland and the north-western interior edge of the Namib and adjacent south-western Angola.

The utilization of colour variation on its own in recognising two subspecies in *F. adspersus* as envisaged by Meyer de Schauensee raises difficulty as birds every bit as dark and densely barred below as those of the Damaraland highlands (topotypical *F. adspersus*), and particularly those of the Waterberg of Namibia (see Clancey 1989), are present in the north-eastern aspects of the species' range in the mid-Zambezi drainage. On the disposition of colour variables on their own, nominate *F. adspersus* requires to be viewed as a polytopic subspecies, its two parts sundered by interposed elements of the lighter, desertic *kalahari*, this finding presupposing that the lighter colouration of the latter is in large part both edaphic and reduced humidity level related. A parallel case is to be found in the Orange River Francolin *Francolinus levaillantoides* (Smith), 1836, which occurs sympatrically with *F. adspersus* over part of its range. *F. levaillantoides* is singularly responsive to variation in the colour and texture of its immediate substrate (see Hoesch & Niethammer 1940) in the more arid parts of its range from northern Botswana to Namibia, and to higher rainfall (and humidity) levels in the mesic grasslands of the eastern plateau in the Transvaal and Orange Free State. Apart from francolins, the assumption of lighter and often less densely streaked plumage is manifest in a wide range of both polytypic non-passerines and passerines affecting the same ecogeographical belt disposed along the northern parts of the South West Arid Zone of the Afrotropics. This transitional zone is in effect a major ecotone, interposed as it is between the steppe-like and karoo conditions present to the south and the mesic woodland savanna — the so-called Miombo — of south-central Africa distributed immediately to the north of it.

In his original description of *F. a. kalahari* Meyer de Schauensee alluded to a rather shorter bill as a possible subspecific character. Measurements assembled for the present research showed that bill-length varied irregularly, perhaps seasonally, throughout the range of the species and could not usefully be used as a taxonomic character. However, the Red-billed Francolin does show interesting and marked variation in size, which is obscured to an extent by the wide differences existing between the wing-lengths of adults and sub-adults in males and the close similarity between adult females and sub-adult (first year) males in their wing-length. Mensural data reveals that males of nominate *adspersus* from the western segment of its disrupted range (in Namibia) are in the main larger than those of the desertic *kalahari* from the north of the territory and Botswana, and, of some significance, from those of its north-eastern population, with which they agree in colouration. Wings in adult males of *F. a. adspersus* measure 190–201+ (195.0), of sub-adults 178–188 (183.8), versus 179–190 (184.3) and 170–177.5 (173.6) mm in *kalahari*. In-

terestingly, a comparable size difference does not show up in the case of both adult and sub-adult females as shown in Table 1. The high variability of tail-length in all populations limits the use of this statistic in research. Much of it is age related, but not always clearly so, and in so far as mensural variation is concerned I have restricted usage here to an interpretation of wing-length data alone.

In concluding that *F. a. kalahari* warrants recognition as a continuously distributed xeric subspecies of desertic country discrete from nominate *F. adspersus* on colour and size grounds, consideration also requires to be addressed to the interesting question as to how *F. a. adspersus* came to have its range split by intrusive elements of *kalahari*. The contemporary combination of plumage and mensural variables of subspecific import in large derives from distant events in the species' evolutionary history, and interaction between onsets and later declines in alternating climate patterns, which, over the millennia, have materially influenced the entire biota of the region inhabited by the present francolin. This lies across the northern parts of a vast arid and semi-arid zone of very long standing. It is posited that in all probability the dark coloured and heavily banded nominate form populations evolved and spread territorially during a mesic climatic phase to later shrink and fragment in the face of the onset of extreme aridity, which, however, favoured the colonization of territory so vacated by desertic phenotypes moving in from country bordering the Namib to the west. The size reduction here shown to occur in the males of the north-eastern segment of *F. a. adspersus* may be either the result of geneflow from contiguous elements of *F. a. kalahari* or a completely independent response to local ecological influences. It is significant that taxonomically relevant variation in size is restricted to males, which, uniquely, is more marked in the case of birds in sub-adult dress. As shown in Table 1 the coefficient of difference in adult males falls just below the conventional limit for the recognition of subspecies (1.28), whereas in subadults the C.D. value is 1.42.

A final decision to recognise *F. adspersus* as a polytypic francolin must seemingly very largely rest on a combination of colour and ventral barring criteria, with the minor size-difference in males of secondary significance, as briefly summarized in the following arrangement of the populations:

a) *Francolinus adspersus adspersus* Waterhouse, 1838: upper Kuiseb River, western Damaraland, Namibia.

Crown Sepia (Ridgway 1912); dorsum and wings similar, the light interstices in the vermiculated pattern Tawny-Olive. On the underside with narrow dark grey transverse barring relatively broad and closely set, especially over the upper breast. Lower abdominal and thigh feathers deep buffy grey, coarsely freckled with a darker shade. Size large in males: adults with wings 191–201+, sub-adults 178–188 mm (Namibian population). Eastern populations with wing-lengths in males as in *F. a. kalahari*.

Range: The plateau of Namibia from the mid-Great Fish R. at Seeheim, north to Damaraland, and with a detached population present in the mid-Zambezi drainage from the eastern Caprivi Strip to south-western Zambia and north-western Zimbabwe (this not separable on the male size character from *F. a. kalahari*).

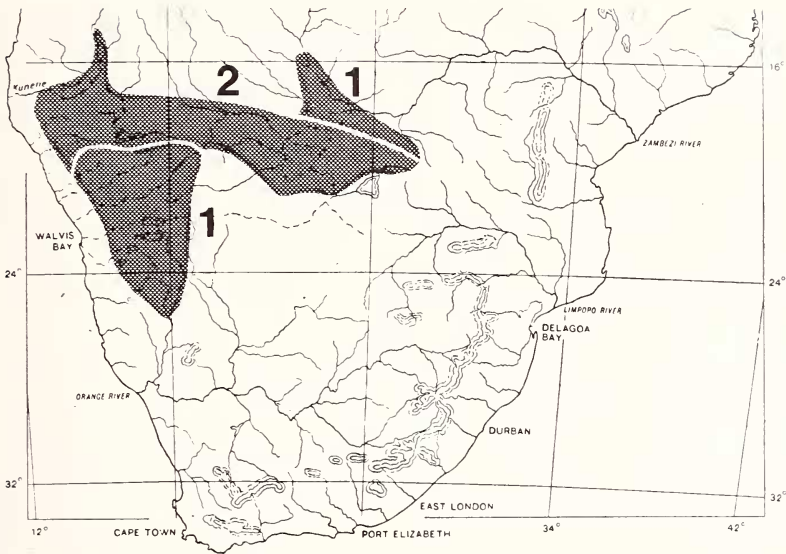


Fig. 1: Sketch-map of Southern Africa showing the range of the Red-billed Francolin and the disposition of the two races: 1. *Francolinus adspersus adspersus* Waterhouse, 2. *Francolinus adspersus kalahari* de Schauensee.

Remarks: The triad of southern African scaled and barred francolin species: *F. capensis*, *F. natalensis* and *F. adspersus*, comprises in the main allopatric taxa, but with marginal range overlap between *natalensis* and *adspersus* occurring in parts of north-western Zimbabwe, south to ca 19° 30' S. There is no indication that they hybridize at this point of contact (see Irwin 1981).

b) *Francolinus adspersus kalahari* de Schauensee, 1931: Lake Ngami, north-western Botswana

Francolinus adspersus kalaharicus Macdonald, 1957 (lapsus).

Paler and buffier over the crown than last, and dorsum and wings lighter and greyer in series (about greyish Buffy Brown, the pale interstices Pinkish Buff). Ventral barring paler grey and not so closely set, especially on the breast, the pallid interstices whiter; abdominal and thigh feathering whiter and less freckled. Size smaller in case of adult and sub-adult males: adults, wings 179–190, sub-adults 170–177.5 mm. Range: Kaokoland and adjacent north-western Namibia and south-western Angola in Mossamedes and Cunene, east to western Caprivi and the Okavango Swamp region of Botswana, south to Lake Ngami and east to the periphery of the Makgadikgadi Pan and the arid course of the Nata R. in the extreme east. See Map 1. Remarks: The character of heavier whitish barring to the hind neck and upper mantle given in the original diagnosis of *kalahari* is inconstant in both subspecies and largely one of immaturity.

While shown as reaching near to the western limits of the Transvaal in Snow (1978), Kemp et al. (1985) state that "there are no confirmed records of this species

(*adpersus*) occurring in the Transvaal", available records in the literature resulting from confusion with *F. natalensis*. Confusion with sub-adult *F. capensis* probably also resulted in the recording of *adpersus* from the lower Orange R. in Snow (1978).

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Zusammenfassung

Francolinus adpersus, der Rotkehlfrankolin, ist die am stärksten xerophile Art aus einer in ihrer Verbreitung auf das südliche Afrika beschränkten Gruppe von drei Frankolinhühnern (*Francolinus capensis*, *F. natalensis*, *F. adpersus*), die durch Schuppen- oder Querwellenzeichnung des Gefieders der Unterseite gekennzeichnet ist. Abgesehen von Meyer de Schauensee, der 1931 nach drei Exemplaren aus dem Gebiet des Ngami-Sees in Botswana eine Subspezies *Francolinus adpersus kalahari* benannte, haben die meisten Autoren *F. adpersus* für eine monotypische Art gehalten. Eine neue Untersuchung größeren Materials zeigte nun, daß blaß gefärbte Stücke wie die, auf die Meyer de Schauensee den Namen *F. a. kalahari* gründete, nicht auf das Gebiet des Ngami-Sees beschränkt sind, sondern westwärts bis Nordwest-Namibia und bis zum mittleren und unteren Kunene in Angola vorkommen und sich damit zwischen dunkler gefärbte Populationen im Süden (Hochland von Namibia) und im Nordosten (Sambesigebiet) schieben, deren erstere sich durch etwas bedeutendere Größe der ♂ auszeichnet; auf sie gründet sich der Name *adpersus* Waterhouse, 1838.

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